Chapter 16

Signaling and Integration of Defense Functions of Tocopherol, Ascorbate and Glutathione

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Summary

Ascorbate, glutathione, and tocopherol are the three major low molecular weight antioxidants of plant cells. While tocopherol is hydrophobic and is found only in lipid membranes, ascorbate and glutathione are hydrophilic, accumulating to high concentrations in the chloroplast stroma and other compartments of the plant cell. Ascorbate and glutathione not only limit photo-oxidative damage but can also act independently as signal-transducing molecules regulating defense gene expression. Both metabolites transmit information concerning oxidative load and redox-buffering capacity. Ascorbate modifies the expression of chloroplast genes. Net glutathione synthesis during stress restores the cellular redox state and allows orchestration of systemic acquired resistance. The degree of redox coupling between these antioxidants has profound implications for regulation, function, and signaling associated with the two major energy-generating systems, i.e. photosynthesis and respiration. Tocopherol fulfills an essential protective function, counter-acting the harmful effects of singlet oxygen production at photosystem II. Ascorbate reduces and thus regenerates oxidized tocopherol, but flux through this reaction is not sufficient to maintain the reduced tocopherol pool under high light stress. This may be because tocopherol regeneration draws on the ascorbate pool of the chloroplast lumen, which may be depleted under stress. Moreover, while glutathione always reduces oxidized ascorbate (dehydroascorbate), the degree of coupling between the ascorbate and glutathione redox couples is variable. The flexibility of coupling between these antioxidant pools is crucial to differential redox signaling, particularly by ascorbate and glutathione.

I. Introduction

Plants are autotrophic organisms fueled by light-driven redox chemistry (Noctor et al., 2000). Through the necessity of harnessing light energy to drive photosynthetic metabolism, plants have optimized strategies for redox control, including ways of minimizing the generation of reactive oxygen species (ROS) and employing a network of pathways of ROS detoxification. Moreover, redox signals exert extensive control on gene expression, adapting plant growth and development to environmental inputs and cues.

Oxygenic photosynthesis and aerobic respiration are both able to undertake the concerted, four-electron exchange between water and oxygen, at photosystem II and terminal oxidases, respectively. In addition, electron transport reactions associated with both processes are a major source of ROS in plants, generating superoxide, hydrogen peroxide, and singlet oxygen (Endo and Asada, this volume). Large amounts of hydrogen peroxide are also formed by the photorespiratory pathway (Foyer and Noctor, 2003), and many other metabolic processes in plants catalyze only partial reduction of oxygen, thus generating superoxide and hydrogen peroxide (Foyer and Noctor, 2000; Mittler, 2002). For example, superoxide and/or H_2O_2 are generated at significant rates by oxidative phosphorylation, fatty acid β-oxidation, and also by many types of oxidase activity. One of the most intensively studied of these pro-oxidant events is the oxidative burst that occurs in the apoplast in response to pathogen attack (Lamb and Dixon, 1997).

There is no doubt that oxygen is potentially toxic and that excessive ROS production is incompatible with cell functions. However, aerobic organisms have evolved means of using the strong oxidizing potential of the O_2/H_2O redox couple ($Em_7 = +\ 815$ mV) in a controlled fashion and, furthermore, also exploit the reactivity of ROS in plant metabolism, signaling, and defense. The roles of ROS in stress-induced damage have long been recognized, but it is now also generally accepted that ROS are an integral component of cellular signaling in both animals (Hancock et al., 2001) and plants (Vranova et al., 2002a, b; Mittler, 2002; Foyer and Noctor, 2003). ROS are involved in innate immune responses in plants as well as in acquired resistance to biotic and abiotic stresses (Alvarez et al., 1998; Dat

Abbreviations: ABA – abscisic acid; AO – ascorbate oxidase; APX – ascorbate peroxidase; DCMU – 3-(3, 4-dichlorphenyl)-1, 1-dimethylurea; DHA – dehydroascorbate; DHAR – dehydroascorbate reductase; FBPase – fructose-1, 6-*bis*phosphatase; G6PDH – glucose-6-phosphate dehydrogenase; GLDH – galactono-1, 4-lactone dehydrogenase; GPX – glutathione peroxidase; GR – glutathione reductase; GRX – glutaredoxin; GSH – reduced glutathione; GSSG – glutathione disulfide; GST – glutathione *S*-transferase; HPP – hydroxymethylphenyl pyruvate; MDHA – monodehydroascorbate; MDHAR – monodehydroascorbate reductase; NAT – nucleobase L-ascorbic acid transporters; NPR1 – nonexpressor of PR genes 1; NCED – 9-*cis*-epoxycarotenoid dioxygenase; PHGPX – phospholipid hydroperoxide glutathione peroxidase; PR – pathogenesis-related; PRK – phosphoribulokinase; PRX – peroxiredoxin; PS I – photosystem I; PS II – photosystem II; ROS – reactive oxygen species; SA – salicylic acid; SBPase – sedoheptulose-1, 7-*bis*phosphatase; TRX – thioredoxin.